

TOOTH WEAR AND ENAMEL STRUCTURE IN THE MANDIBULAR INCISORS OF SIX SPECIES OF KANGAROO (MARSUPIALIA: MACROPODINAE)

WILLIAM G. YOUNG, MICHAEL STEVENS AND ROBERT JUPP

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Tooth wear and enamel ultrastructure of the mandibular incisors of six macropod species were investigated using plain and polarized light microscopy and scanning electron microscopy. Three modes of wear occurred on these teeth; (i) abrasive wear on the incisal edge; (ii) attritional wear on the medial edge; and (iii) occlusal wear on parts of the incisal edge. The first two modes of wear relate to the known mastication of the macropods. Possible causes of the third are discussed. The enamel structure of the teeth is complex and shows several distinct features: zones within the enamel, a distinct bend in the prisms which overall are oriented antero-laterally; prism decussations and whorls. These features are interpreted as either wear retardants or possible adaptations to minimize damage on fracture. The latter interpretation is based on the loading experienced by these teeth and the known physical properties of enamel and dentine in relation to the behaviour of anisotropic materials and crack propagation theory.

□ *Tooth wear, enamel ultrastructure, Wallabia, Macropodinae, Macropus, Proteomodon.*

William G. Young, Michael Stevens and Robert Jupp, Department of Oral Biology and Oral Surgery, University of Queensland, St. Lucia, Qld 4076, Australia; 30 November, 1988.

The procumbent mandibular incisor is the hallmark of diprotodont marsupials. Its form and function are distinctive in the Macropodinae. The lateral margin of the crown forms an incisal edge that occludes with the three maxillary incisors, for a relatively greater length than in the closely related possums (Phalangerinae). Much of the medial edge abuts its counterpart over a ventral, interproximal contact area.

Using cinematographic and cineradiographic techniques, Ride (1959) found that the medial edges of the mandibular incisors of Bennett's Wallaby, *Macropus rufogriseus fruticus*, abut in the resting position, lying within the maxillary incisal arcade. The movable mandibular symphysis, and mandibular protraction allow a slight separation of the mandibular incisors to bring them simultaneously into occlusion with the premaxillary ones. Food, such as grass, is gripped and detached with a jerk of the head; it is apparently not incised. Harder objects such as carrot, cause greater separation. A scissoring action, employing the medial edges (Murie & Bartlett, 1866), has not been observed. It is possible that this variation of mandibular incisor position permits full occlusion during incision or allows the mandibular incisors to clear their maxillary

counterparts during lateral, anisognathous molar chewing movements (Ride, 1959).

Tooth wear, be it abrasion (food to tooth) or attrition (tooth to tooth), has been used to determine the relative direction of jaw movements and the nature of occlusion in a number of mammalian species. The diagnostic wear and microwear features are facet location, polish, striation orientation, pitting and the asymmetry of the enamel to dentine interfaces of the leading and trailing dentine profiles (Greaves, 1973; Rensberger, 1973; Gordon, 1984; Walker, 1984; Young & Marty, 1986; Young & Robson, 1987).

Microwear features often reveal how the underlying enamel ultrastructure has been adapted, by selection, to resist various forms of wear (Rensberger, 1978; von Koenigswald, 1980; Fortelius, 1985; Boyde & Fortelius, 1986; Young, McGowan & Daley, 1987). Variations in the course of enamel prisms from the enamel-dentine junction (EDJ) to the surface are probably adaptations to resist wear and fracture (Rensberger & von Koenigswald, 1980; Boyde & Fortelius, 1986).

The complexity of the mandibular incisor enamel of macropods has long been recognized (Owen, 1840-1845; Tomes, 1849; Carter, 1920; Williams, 1923; Beier, 1983). Principally, the prism orientation undergoes a marked change a short

distance from the EDJ. Schmidt and Keil (1971), using polarized light microscopy, noted three zones in macropod mandibular incisors, evidently the result of changes in hydroxyapatite crystal orientation. Zone 1 extends from the EDJ to a prominent directional change; Zone 2 from that directional change to a colour interdigitation; and Zone 3 from the interdigitation to the outer surface. A scanning electron microscopic (SEM) study of the enamel of 14 macropod species found that vertical decussations (Hunter-Schreger bands) occur at locations subject to excessive wear, such as incisal edges, shearing premolar blades and the occluding surfaces of molar lophs. The presence, extent, or absence of decussations seems to be related to the degree of enamel attrition (Beier, 1983). Lester *et al.* (1987), also using SEM, found that within the lateral and medial enamel of the mandibular incisors of *Macropus eugenii* there is, in addition to the prominent change in prism direction, a region of gnarled enamel. These ultra-structural features could be, to some extent at least, adaptations to resist wear and perhaps to prevent fracturing under load (Rensberger & von Koenigswald, 1980). This study examined the microwear and ultrastructure of the incisal and medial edges of mandibular incisors from several macropod species to (a) determine the mode of wear, and (b) further document the enamel ultrastructure and its variability. Where possible the wear and microwear on the matching maxillary incisors was also examined.

MATERIALS AND METHODS

Mandibular incisors of the following species (with status and number of teeth in brackets) were used in this study: *Wallabia bicolor* (extant — 2); *Macropus rufogriseus* (extant — 4); *Macropus giganteus* (extant — 1); *Macropus siva* (extinct — 1); *Macropus titan* (extinct — 1); *Protemnodon* sp. (extinct — 1).

SCANNING ELECTRON MICROSCOPY

Epoxy resin replicas of each tooth were produced by the method of Waters and Savage (1971) and Grundy (1971). These were cut longitudinally with a wheel on a microlathe to separate lateral and medial surfaces, then mounted uppermost on stubs and gold sputtercoated for SEM examination. Where possible the maxillary incisors were also prepared for SEM. Microwear features were recorded with a Phillips 505 SEM at 15-300X

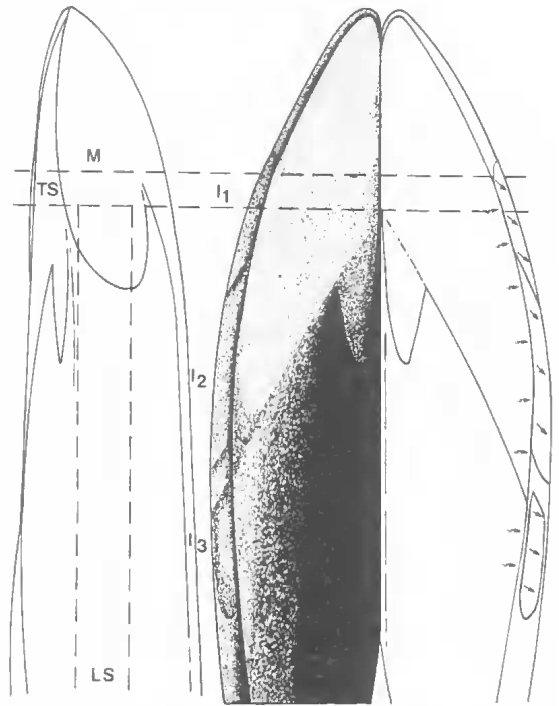


FIG. 1. Left: Medial aspect of left mandibular incisor. Right: dorsal aspect of both left and right mandibular incisors of a macropod (in this case, *Macropus rufogriseus*) illustrating where the various sections were taken, and the location of facets and striations. TS, transverse section; LS, longitudinal section; M, interproximal attrition facet; I1, I2, I3, the facets caused by occlusion with maxillary incisors; Bent arrow, direction of abrasion striations on dentine and incisal enamel; Straight arrows, attrition striations on occlusal facets.

magnification and are described using the terminology of Rensberger (1978). The actual teeth were sectioned for light microscopy (see below). The remaining portions of the incisors were embedded in an acrylic based resin (L.R. White), polymerized in an argon atmosphere for 48 hours at 55°C. These were then mounted, ground, polished, etched in 3% phosphoric acid for 90s and finally gold-coated for examination at 15-1000X magnification. Surface-parallel windows were similarly prepared to view the unworn enamel underlying the incisal and medial edges.

TRANSMITTED LIGHT MICROSCOPY

Each tooth was sectioned transversely, midway along the enamel crown and perpendicular to the unworn posterior incisal edge. A longitudinal section, normal to the first, was then taken parallel to the medial edge and midway between it and the

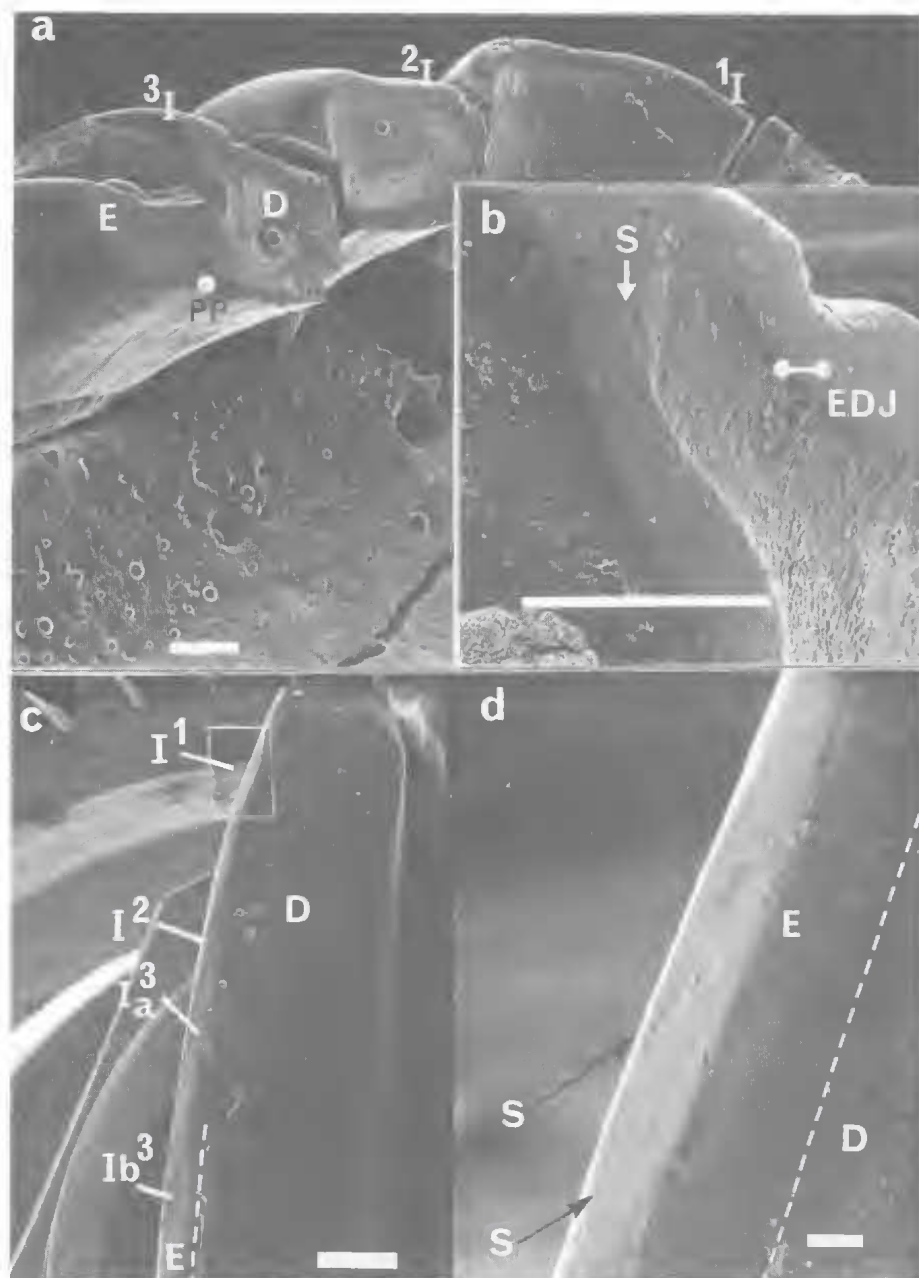


FIG. 2. (a) Scanning electron micrograph (SEM) of a replica of the three right maxillary incisors of *Macropus rufogriseus* showing the occlusal surfaces. E, attrition wear on enamel edges; D, abrasive cavitation of exposed dentine; PP, flaked pits on lingual aspect of the enamel edge; ¹I, central maxillary incisor; ²I, second maxillary incisor; and ³I, third maxillary incisor. Note the exaggerated labial groove on ³I. Scale bar = 1 mm. (b) Enlargement of ³I. S, parallel striations orientated antero-medially on enamel incisal edge; EDJ, enamel-dentine junction showing the gentle transition on labial side. Scale bar = 0.5 mm. (c) SEM of a replica of the incisal edge of the mandibular left incisor of *Macropus rufogriseus*. D, exposed dentine; E, enamel edge; ¹I, ²I, ³Ia and ³Ib indicate rhomboidal attrition facets due to occlusion with the central, second, anterior aspect of the third, and posterior aspect of the third maxillary incisors respectively. Scale bar = 1 mm. (d) Enlargement of 2c. E, the convex, abraded enamel edge; D, exposed dentine; S, anteromedial, parallel striations on the attrition facet (¹I); dotted line represents EDJ. Scale bar = 0.1 mm.

incisal edge (Fig. 1). These sections were mounted on glass slides with cyano-acrylate adhesive and ground to a thickness of 70 to 100 microns (μm) with progressively finer silica and alumina grits on a Buehler polisher. After cleaning and drying, the sections had a cover slip attached with a polystyrene mounting medium. Plain and polarized light microscopy was conducted using a Leitz Orthomat microscope equipped with a polarizing objective and a quarter wave plate. Linear dimensions, where applicable, were determined with a calibrated eyepiece micrometer, accurate to one μm . Tubule and prism angles in relation to the EDJ were measured with an eyepiece protractor accurate to one degree. Wear and microwear features were recorded from SEM micrographs of the replicas. The three-dimensional organization of the enamel ultrastructure was determined using a combination of transmitted plain and polarized light microscopy and SEM microscopy of the polished and etched sections.

RESULTS

TOOTH WEAR

All maxillary incisors available for study, have broad incisal facets on their incisal surfaces (Fig. 2). Parallel striations, orientated antero-medially, traverse the labial enamel, whereas flaked pits are found on the lingual enamel (Figs 2a & b). The profile between enamel and dentine surfaces is relatively gentle labially but dentine is hollowed out in front of the lingual enamel (Fig. 2).

The enamel on the labial incisal edge of the mandibular incisors is smoothly convex and traversed by fine striations directed more or less laterally. This rounded edge is interrupted by several well defined, relatively flat facets which correspond to the upper incisors (Figs 1 and 2). These facets are traversed by parallel, antero-medially oriented striations (Fig. 2). In the case of *Wallabia bicolor* and *M. rufogriseus*, a distinct labial groove in the third maxillary incisor effectively divides the occluding surface of that tooth. Thus in these two species, two facets are found on the mandibular incisor which corresponds to this feature on the third maxillary incisor.

The medial edges of the mandibular incisors are flat, well-defined facets (Figs 3a, b & c). The microwear on the enamel comprised many small pits and short striations of random orientation (Fig. 3).

Three modes of wear are, therefore, represented on the mandibular incisors:

- (a) well-rounded incisive edges traversed by predominantly parallel, striations oriented in a lateral direction;
- (b) well-defined rhomboidal facets along the incisal edge, traversed by parallel, antero-medially aligned striations; and
- (c) well-defined interproximal facets with extensive pitting and short striations of variable orientation.

ENAMEL STRUCTURE

In all the species studied, the dorso-lingual surface of relatively unworn mandibular incisors is virtually free of enamel (Fig. 3a). The labial surface enamel is approximately uniform in thickness, whilst the medial surface varies in thickness. The incisal enamel edge is generally convex. The prisms of the mandibular incisor enamel are arranged in closely packed parallel arrays and are separated by distinct interprismatic sheets (Fig. 4). The crystals of the sheets do not intrude between the prisms of an array. In cross-section, the prisms are oval, their greatest and least widths being 5 μm (parallel to the sheets) and 2-3 μm respectively. Sheet widths average 1.7 μm (Figs 4b, c & d). Generally, the prism axis coincides with the long axis of the crystals. In the region of the incisal and medial edges, however, the crystals are aligned at about 25° to the prism axis and are approximately normal to the tooth surfaces. The sheet crystals are aligned at 85-95° with respect to those in the adjacent prisms. Enamel tubules are best seen when they are represented as artificial casts in resin embedded sections. Tubules are present only in the prisms, or immediately adjacent to them, and thus follow the same course (Fig. 3b).

Four additional ultrastructural differentiations are found within the mandibular incisor enamel. Three of these, overall change in prism orientation, zoning, and prism decussation, are present in all the species examined. The fourth, whorled enamel, although present in all six species, differs in its location. Although these differentiations are discussed below separately, they are often interrelated. For example, zoning is largely the consequence of change in prism orientation.

PRISM ORIENTATION

The inner labial enamel, viewed in longitudinal section, is composed of a series of parallel prisms and sheets, aligned antero-laterally and departing from the EDJ at 60-100° (Fig. 4). A short distance out from the EDJ there is an abrupt directional

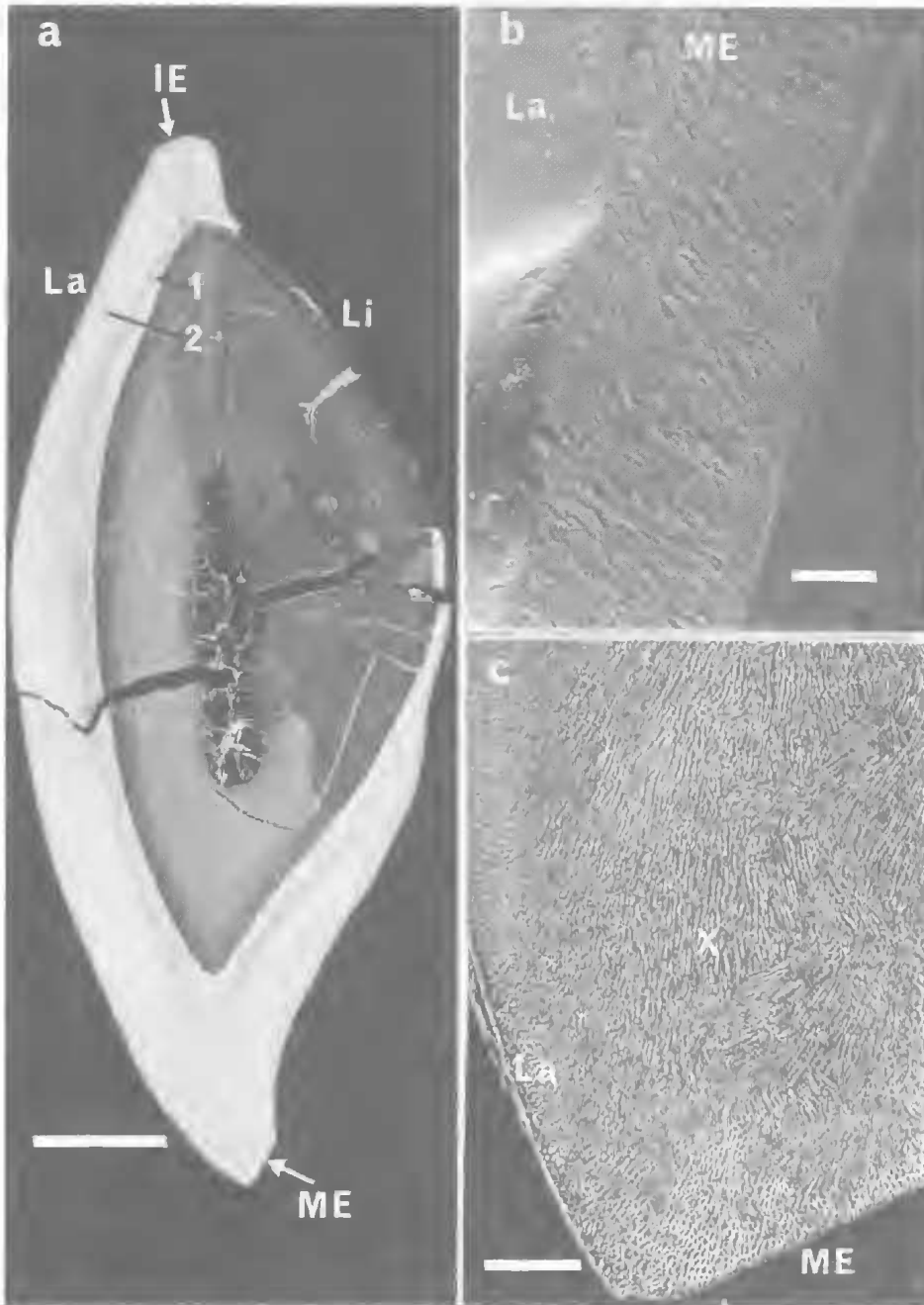


FIG. 3. (a) Light micrograph of transverse section of mandibular incisor of *Macropus giganteus*. IE, relatively unworn incisal edge with convex profile, the "arrowed" portion being an attrition facet due to occlusion with a maxillary incisor; La, labial enamel approximately 700 μm thick (note artefactual crack along the prism interface that changes direction between zones 1 and 2); 1, zone I narrowing towards the incisal edge; 2, zone II of approximately uniform thickness; Li, lingual aspect of tooth devoid of enamel; ME, medial attrition facet. Scale bar = 1 mm. (b) SEM of medial edge enamel. ME, interproximal facet with pitted texture indicating compressive wear; La, labial enamel. Scale bar = 0.2 mm. (c) SEM of an etched section of the most ventral enamel. La, labial surface; ME, medial edge attrition facet; X, extensive prism decussation. A similar pattern of decussation was found in the incisal edge enamel. Scale bar = 0.1 mm.

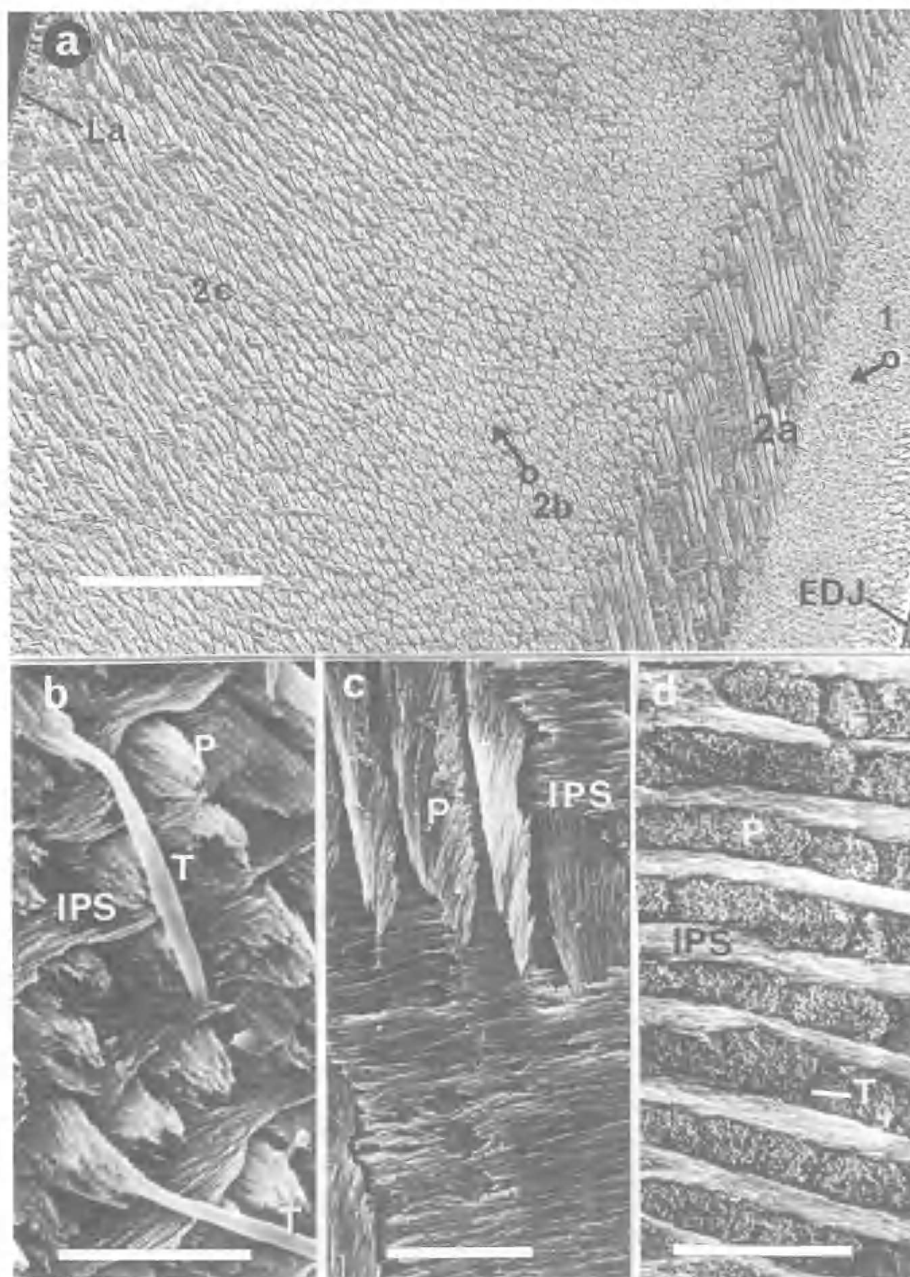


FIG. 4. (a) SEM from an etched transverse section of labial enamel of *M. giganteus*. EDJ, enamel-dentine junction; La, labial enamel; I, zone I with prisms cut transversely and aligned posteroventrally (2a). A marked change of direction, a 90° bend occurs between zones I and II. In the inner region of zone II the prisms are aligned dorso-laterally and anteriorly (2b); in the outer region of zone II (2c) the prisms are similarly oriented but now assume a less anterior alignment. Scale bar = 0.1 mm. (b) SEM from an etched transverse section of the enamel of *Macropus rufogriseus*. P, prism; IPS, interprismatic sheets; T, cast of tubule, an artefact of epoxy resin embedding. Scale bar = 10 μ m. (c) SEM from an etched longitudinal section of the incisal enamel of *Macropus rufogriseus*. P, prism; IPS, interprismatic sheets. In this orientation the tubules are not readily apparent. Scale bar = 10 μ m. (d) SEM of an etched transverse section of the incisal enamel of *Macropus rufogriseus*. P, row of prisms; IPS, interprismatic sheets; T, tubule. Scale bar = 10 μ m.

change to a more anterior orientation of 45-60° relative to the EDJ. This change in direction delineates zones I and II (see below and Fig. 5b). In transverse sections, the inner labial prisms are ventro-laterally aligned and at 135-155° to the EDJ. At the point of directional change, the prisms turn, through 90-100°, thus aligning dorso-laterally at 30-55° relative to the EDJ.

ZONING

Zoning, which is primarily a consequence of the overall change in prism orientation, occurs in the labial, and, to a lesser extent, in the medial enamel. Two main zones are evident. Zone I extends from the EDJ to, and is delimited by, the abrupt change in prism direction. Zone II is composed of the remaining outer enamel (Fig. 4a). This zone may be further subdivided into inner and outer regions on the basis of a more subtle ultrastructural differentiation (see below). The ratio of the thickness of zone I to the overall enamel thickness exhibits interspecific variation (Table 1).

On the labial enamel zone I is of approximately uniform thickness. At its more dorsal (incisal) extremity, zone I narrows somewhat, whilst ventrally it broadens and becomes ill-defined (Fig. 3a). Zone II, when viewed with transmitted polarized light, appears to have a distinct inner and outer region. Delineating these two regions is a boundary of interdigitating colors. This boundary is found to correspond to the position of enamel prisms in a whorled arrangement (see below). The inner and outer regions of zone II probably correspond to zones two and three of Schmidt and Keil (1971).

PRISM DECUSSATION

Within the incisal and medial edges decussating arrays of prisms (i.e. parazonal and diazonal), are present and overlap each other at obtuse angles (Figs 3c and 5d). This arrangement probably corresponds to the gnarled enamel of Lester *et al* (1987).

WHORLED ENAMEL

In the smaller kangaroos, (*Wallabia bicolor* and *M. rufogriseus*) mid-labial, subsurface sections reveal regions of whorled enamel (Figs 5a and c), which in oblique transverse section are prisms arranged in spirals. This feature does not manifest itself at the tooth surface. Rather the prisms resume their parallel lateral course towards the incisal edges before terminating in the aprismatic region immediately below the surface. Whorled enamel

TABLE 1.

Species	Zone I thickness : Total thickness
<i>Macropus rufogriseus</i>	1/6 to 1/5
<i>Wallabia bicolor</i>	1/6 to 1/5
<i>Protemnodon</i> sp.	1/6 to 1/5
<i>Macropus siva</i>	1/5 to 1/4
<i>Macropus titan</i>	1/4 to 1/3

also occurs in the other species studied but, is found well below the incisal and medial surfaces.

DISCUSSION

Our observations of macropod enamel structure confirm and amplify those of previous workers. This discussion attempts to relate modes of wear to details of enamel structure, and suggests how the main ultrastructural differentiations may be adaptations to the wearing forces.

TOOTH WEAR

Three modes of wear occur on the mandibular incisors. Two of these are readily explained by recognized functions. The convex contour to, and generally lateral striations on, the incisal enamel edge are almost certainly due to cropping. The lateral striations could result from siliceous grasses or particles being dragged across the outer dentine and enamel edge as the head pulls back to divide the grass. Such attrition can cause considerable wear in cropping (Young & Marty, 1986).

The medial facets with their extensive pitting and short, randomly-aligned striations, appear to be the result of compressive attrition. This occurs when grasses and extraneous materials are trapped between the constantly closing and spreading mandibular incisors. Facet microwear due to attrition of this nature is found in other taxa (Young & Marty, 1986).

The third mode of wear, distinct rhomboidal wear facets with striations aligned antero-medially, is not explicable by the type of cropping observed in cinefluorography by Ride (1959). It is possible that an anisognathous incision is also employed, in addition to the isognathous cropping action of the incisors. The antero-medial orientation of the striations indicates that the action is unilateral. The enamel-dentine transition on the maxillary incisal edges is smooth labially and relatively abrupt lingually. This shows that the direction of this action is a labial to lingual occlusal movement (Greaves 1973). Another explanation could be that the inter-incisal attrition facets occur as an

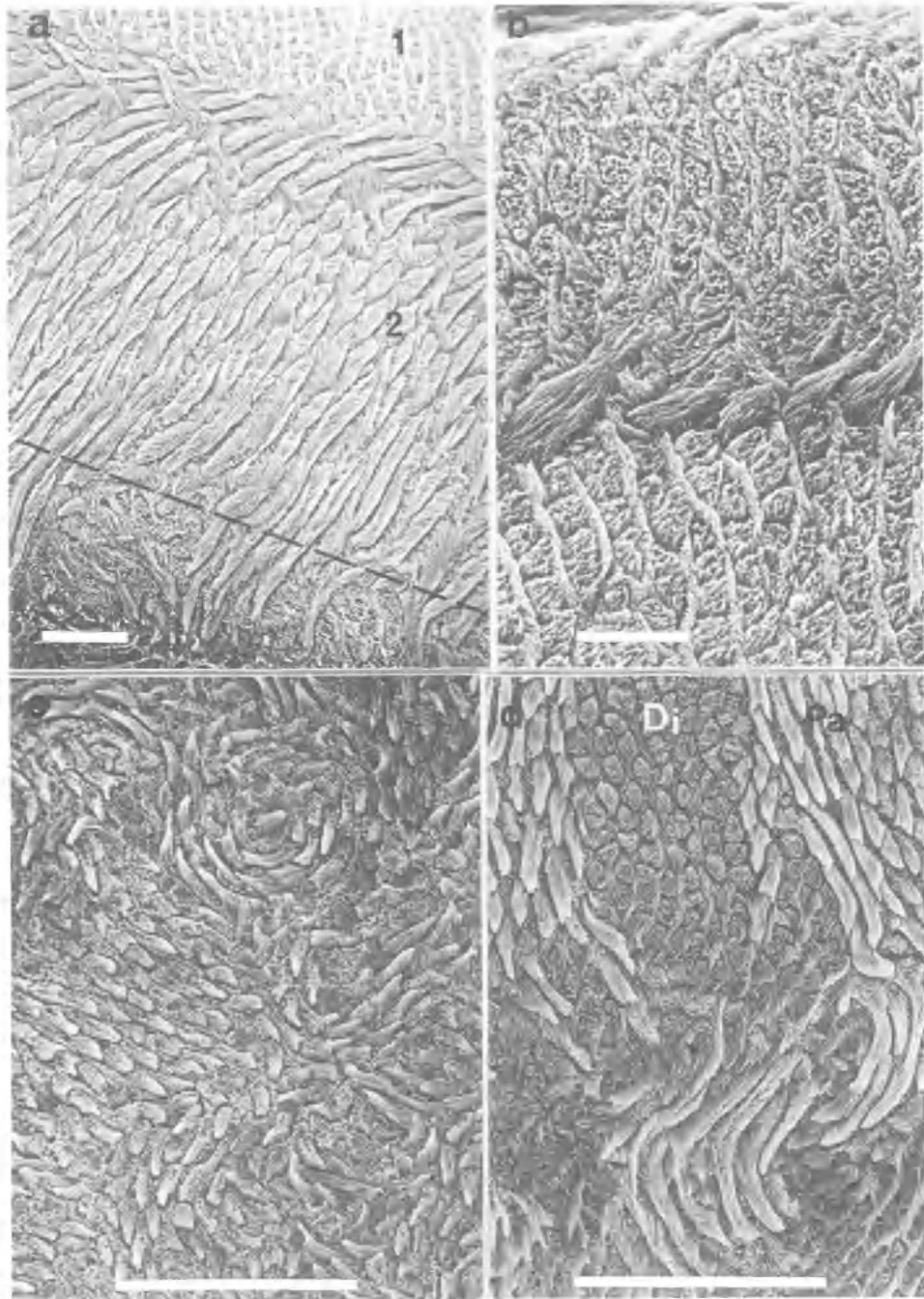


FIG. 5. (a) SEM of an etched longitudinal section of the incisal enamel of *Wallabia bicolor*. 1, zone I enamel prisms cut transversely; 2, zone II enamel prisms cut in oblique longitudinal section. Anterior to left. At the dashed line, a surface parallel window has been cut perpendicular to the longitudinal section, revealing location of the whorled pattern (cf. 4c). Scale bar = 20 μm . (b) SEM of etched longitudinal section of the incisal enamel of *Macropus rufogriseus*. Showing the prism bend. Anterior to left. Scale bar = 10 μm . (c) SEM of an etched, sub-surface section of the lateral incisal enamel of *Wallabia bicolor*. Clearly showing whorled enamel. Scale bar = 10 μm . (d) SEM of an etched, sub-surface section of the incisal edge enamel of *Macropus rufogriseus*, showing prism decussation (Hunter-Schreger bands). Di, diazone; Pa, parazone. Scale bar = 10 μm .

incidental consequence of the antero-medial chewing action of the molars. However, the mandibular incisors appear to be able to clear their maxillary counterparts when approximated (Ride, 1959), and thus this seems an unlikely possibility, despite the observation that chance glancing contacts can be produced by manipulation of dried skull and jaws.

ENAMEL STRUCTURE

One feature which dominates the differentiation of macropod enamel ultrastructure is the abrupt directional change in prism orientation resulting in zoning.

Such distinct zones do not occur in two other diprotodont marsupials which have procumbent mandibular incisors, the Koala *Phascolarctos cinereus*, and the possum *Trichosurus vulpecula* (personal observation). This suggests that the high degree of enamel differentiation found in the macropod incisors is an adaptation to the functional loads imposed on these teeth by the extent of the incisal edge. Consequently a comparison of these differentiations over a wider range of diprotodontians would be instructive.

Although prism decussation occurs in the labial and medial edges, it does not manifest itself at the surface as a series of troughs and ridges as in rhinoceroses (Rensberger & von Koenigswald, 1980). This suggests either that the decussations are not as well-defined in the macropods, or that they suffer multidirectional abrasion that obliterates any protruding.

The following is a tentative explanation of different prism orientations. Assuming that the main loading on the mandibular incisors results from cropping and anisognathous incision forming the facets, then the major force operating will be applied to the anterior portion of the tooth and lateral to its longitudinal axis. This will cause a torsional stress, and tend to bend the tooth ventrally. Young's modulus, is almost certainly lower for dentine than for enamel, even though the values quoted in the literature are highly variable (e.g. $E_{\text{dentine}} = 7.6 \text{ to } 19.0 \times 10^9 \text{ N.m}^{-2}$ and $E_{\text{enamel}} = 9.6 \text{ to } 84 \times 10^9 \text{ N.m}^{-2}$; Rasmussen & Patchin, 1984). So, for a given stress (load per unit area), the dentine, although thicker, is likely to experience a greater strain deflection. This would be expressed as the fractional change in a linear dimension, or as an angular deflection in (unitless) radians. Thus, during cropping, the torsional stress would cause greater deflection of the dentine than the enamel. The enamel prisms will then experience compressive torsional loading. If this is so, then the

overall postero-ventral orientation of the labial zone II prisms will redirect such loadings in an oblique, circumferential path through the enamel and away from the point of application. In this manner the antero-lateral tooth loadings are redistributed more evenly along the length of the tooth. This may solve one problem but another is introduced. The prism orientation in zone II, seemingly so favourably arranged to redirect compressive torsional loadings in the posterior portion of the teeth, will now undergo a tensile loading in the more dorso-posterior regions of the enamel. Also, the tension will operate more or less at right angles to the prism alignment. The tension failure (i.e. cracking of brittle, heterogenous, anisotropic materials like enamel) occurs preferentially along interfaces (Gordon, 1968). For example, the "work of fracture" value, — i.e. the energy to create new surfaces (by crack propagation) — within enamel, is $0.13 \times 10^2 \text{ J.m}^{-2}$ parallel to the prisms and $2.0 \times 10^2 \text{ J.m}^{-2}$ perpendicular to them (Rasmussen & Patchin, 1984). The artifactual crack in the mandibular incisor of *Macropus giganteus* (Fig. 3a) shows this and demonstrates that the prisms have relatively weak interfaces. This is a necessity for the successful operation of a crack-stopping mechanism (Cook & Gordon, 1964). The existence of prism decussations on the lateral and medial edges and subsurface regions of whorled enamel may represent a solution to this problem. Further, should a crack occur, then upon encountering the whorled enamel, with its multiplicity of non-aligned interfaces, it is likely to be halted by the crack-stopping mechanism. This mechanism simultaneously redirects a crack along an interface approximately normal to the original direction of crack propagation and increases its tip radius by many orders of magnitude. The effect of redirection is that the new alignment is energetically less favourable for opening and thus spreading the crack in terms of the pattern of stress concentrations which spread the original crack. The increased tip radius further lowers stress concentration in the immediate vicinity. This in turn increases the critical Griffith length, beyond which catastrophic failure occurs and which is inversely proportional to the square of the imposed stress (Gordon, 1968). It is also possible that the energy required for the formation of new surfaces (between the separating interfaces) is provided by an equivalent decrease in strain energy and, therefore, in the stress experienced by the system. Either way, the locational differences of whorled

enamel in the species studied may indicate differences in the site of these tension loadings.

There may be two explanations also for the bend in the prisms. Either the bend is a crack deflector, or it represents a developmental necessity, given the possible constraints of enamel formation. As illustrated by Figure 3a, cracks readily follow the relatively weak prism interfaces. Just what is achieved by this is not obvious. Once a crack of external origin has reached the bend, much damage has already occurred. However, the crack will encounter the EDJ more dorsally. Perhaps this is a form of damage control in that, having failed, the enamel ventral to the crack (in danger of breaking away) retains a greater area of attachment to the dentine. If such a mechanism is operating, then it is reasonable to ask why the bend is not closer to the outer surface where these possible benefits would be greatest. The other explanation is that the bend has nothing to do with fracture resistance or crack deflection. Given that prisms can neither bifurcate, nor appreciably alter their diameter, ameloblasts (and therefore the prisms) might be constrained in terms of the angle at which they depart the EDJ. Cell packing or the spatial organization of the Tome's processes might require this. Achievement of the final tooth crown morphology and a suitable ultrastructure (i.e. with the prisms in regions of high wear intersecting the crown surface at suitably obtuse angles) may, in some instances, necessitate this drastic directional change by the ameloblasts.

CONCLUSIONS

The pathways of the prisms in macropod incisor enamel are remarkably regular, three-dimensionally complex, differentiations. A uniform bend in the prisms occurs a short distance from the EDJ on the lateral aspect of the tooth. This may be a device to transmit torsional loads to the dentine. Microwear indicates that the torsional loads probably exist. Further from the EDJ, the prisms spiral in whorls. This may be a device to resist crack propagation along the paths of the prisms. In the lateral incisal edge and on the medial proximal contact edge, the prisms decussate. This may be a device to increase edge strength and to resist compressional loads for the microwear, particularly on the medial facet, where microwear indicates compression. As these differentiations were uniform throughout the macropod species studied, it seems unlikely that differences in the presence or absence of whorls, or in the widths of

zones, for example, could be used for taxonomic separation of closely-related macropods. However, if these differentiations have functional significance, they would be expected to scale allometrically in macropods of different size but similar incisor functions. Examination of these differentiations in a wider range of diprotodonts might therefore be instructive regarding taxonomic interrelationships.

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